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Research Article

Influence of land use intensity on ecological corridors and wildlife crossings' effectiveness: comparison of 2 pilot areas in Austria

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Abstract

Human development and induced activities significantly affect the natural functioning of ecosystems and hence landscape connectivity. Ecological corridors are essential for maintaining structural as well as functional connectivity in cultural landscapes for wildlife, while providing interchange between core areas. In two pilot areas in the north-western and eastern part of Austria, ecological corridors were delineated using a geographic information system (GIS). The pilot areas are key to preserving ecological connectivity and are located along important international migration corridors (Bohemian Forest-Northern Alps corridor, Alpine-Carpathian corridor). Both areas are situated in highly human-altered and therefore dissected as well as fragmented landscapes. A one-year monitoring campaign using camera traps was carried out at selected locations along proposed ecological corridors in the cultural landscape and at wildlife crossings structures (WCSs) at intersections with road infrastructure. The monitoring was focused on mammals with a total of 18 species being observed. The most abundant species were roe deer, European hare and wild boar. European otter, European beaver, golden jackal and wildcat have only rarely been observed. Mammal species richness was positively correlated with the presence of vegetation cover and the coefficient of ecological stability (CES). The insights obtained can be used for recommendations and support in planning the planting of vegetation (use of grasslands, scattered and continuous woody vegetation, agroforestry systems) on the sites and in the vicinity of ecological corridors. The green bridges (wildlife overpasses) were used more frequently as well as by a larger number of mammal species compared to other studied WCSs showing characteristics that are less favourable for animals. The effectiveness of WCSs is mainly influenced by human activities, resulting in the recommendation to limit them on WCSs located along the routes of ecological corridors. We point out that actual wildlife migration corridors are likely to differ from designated data-driven ecological corridors generated by spatially explicit models, because these generally do not take into account all factors relating to the effectiveness of corridors. Our results suggest, that the application of the concept of functional connectivity is able to enhance the quality of ecological corridor designations, since usually they are based only on the concept of structural connectivity. For this reason, further studies are needed to help understanding factors and their specificities influencing the interplay between structural and functional connectivity of ecological corridors.

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Key words: Alpine-Carpathian corridor, Bohemian Forest-Northern Alps corridor, coefficient of ecological stability, daily activity, landscape connectivity, functional connectivity, habitat fragmentation, wildlife crossing structures, wildlife monitoring

Introduction

Landscapes are changing dramatically due to human influences (Gardner et al. 1993; Antrop 2004; Bennett and Saunders 2010). The current state of the landscape is the result of significant changes caused by urban and rural development, the expansion of linear infrastructure and traffic, agricultural intensification, changes in forest management, expansion of energy networks and renewable energy (Antrop 2004; Farinaci et al. 2014; Van Der Ree et al. 2015b; Plieninger et al. 2016). Around 80% of the Earth's land surface currently shows signs of human intervention (Ellis and Ramankutty 2008; Venter et al. 2016a, 2016b) resulting in loss of biodiversity (Butchart et al. 2010) and of the capacity and multifunctionality of ecosystem services (Corvalán et al. 2005). In the EU and UK, almost a third of the land (27%) is highly fragmented where habitats are on average less than 0.02 km^2 (EEA 2022).

Unscathed and coherent natural habitats are gradually being disintegrated by humans into smaller units or spatially disjunct patches (Bennett and Saunders 2010). Fragmentation results in species behavioural changes (Opdam et al. 1993; Tucker et al. 2018) connected with a number of serious problems such as habitat loss (Huxel and Hastings 1999; Brooks et al. 2002), landscape change (Antrop 2004; Leimu et al. 2010; Jarzyna et al. 2015), biodiversity loss and reduced fitness of wild animals due to genetic isolation and inbreeding (Ellegren et al. 1996; Hanski 2011; Lino et al. 2019) leading to wildlife population decline (Bender et al. 1998) or extinction (Andrén 1997; Fahrig 1997; Pardini et al. 2018; Wilkinson et al. 2018) and increased wildlife-vehicle collisions (Morelle et al. 2013; Vanlaar et al. 2019; Saint-Andrieux et al. 2020). Mitigation or so-called defragmentation measures are applied in practice to avoid or minimise the above-mentioned consequences. In order to ensure permanent permeability of the landscape for wildlife, ecological corridors or networks (Jongman et al. 2011; Gregory et al. 2021) and wildlife crossings structures (WCSs) (Ford et al. 2009; Smith et al. 2015) are planned, built and maintained. Ensuring connectivity is among the main contemporary challenges in the protection of nature and landscape (Bennett et al. 2006; Jongman et al. 2011; Keeley et al. 2018).

Ecological corridors are important elements in nature and landscape conservation. They are the backbone of green infrastructure necessary to maintain or restore connectivity, biodiversity and ecological functions in the landscape (Bennett and Mulongoy 2006; Zheng et al. 2019; Gregory et al. 2021). Ecological corridors are usually linear-shaped areas providing connections between native habitats, stepping stones, and interacting features in the landscape while enhancing the ability of wildlife and plants to move between larger core areas (Bennett and Mulongoy 2006; Damschen et al. 2006; Hilty et al. 2020; Gregory et al. 2021). Connecting the remaining habitat fragments plays an important role in maintaining gene flow and genetic diversity for both plants (Sork and Smouse 2006) and wildlife (Waits et al. 2015). WCSs are an important instrument, ensuring the connectivity of ecological corridors through high-density traffic infrastructure. Increasingly, integrated approaches of geographical information systems (GIS) and other software tools are

being used to design and manage appropriate routes for ecological corridors including localization and parameterisation of WCSs. These spatially explicit methods use a number of different algorithms such as cost distance (least-cost path), circuit theory or Euclidean distances (McRae et al. 2008; Suppan and Frey-Roos 2014; Loro et al. 2015; Ribeiro et al. 2017; Zheng et al. 2019; Mardeni et al. 2023). Two different aspects of connectivity should be distinguished, both of which are prerequisites for the success of corridors: in contrast to structural connectivity, which considers the physical characteristics that support connected habitats, functional connectivity can be defined as the degree of specific responses of certain wildlife to elements in the landscape (Koen et al. 2014; Sedy et al. 2022).

The effectiveness of WCSs has already been investigated in many studies (Clevenger and Waltho 2003; Mata 2003; Simpson et al. 2016; Mysłajek et al. 2020). However, most of the studies focused on the effects of size and type of WCS, rather than the characteristics of the location of WCS. Moreover, the majority of existing studies are based only on the number of individuals crossing WCSs and do not account for the number of total approaches (Chambers and Bencini 2015). Denneboom et al. (2021) summarised the results of 77 studies regarding WCS efficiency in a systematic review and meta-analysis. They showed that viaducts are the most effective type of WCS for large mammals and that WCSs built specifically for wildlife are used significantly more than those used by humans in addition to wildlife.

The aim of this work was to conduct monitoring of the occurrence of mammals at designated sites (EEA and Jurečka 2023) along ecological corridors within the cultural landscape and WCSs at crucial intersections with road infrastructure in two pilot areas in Austria. Subsequently, the data of mammal presence and species richness were compared with the current state of the environment near the monitoring sites using the ecological stability coefficient (the ratio of relatively stable areas to unstable areas). The influence of distance to various landscape features (core areas, forested areas, watercourses, water bodies, motorway incl. expressway infrastructure, built-up areas) was also evaluated. The last objective of the work was to identify the permeability for mammals on the studied WCSs located along the routes of ecological corridors designed using an integrated approach employing geographic information systems combined with human activity and width of WCSs.

Methods

a) Ecological corridors: GIS-model

Ecological corridors designated for the Interreg Danube project SaveGREEN, which are located in two pilot areas in Upper Austria as well as at the border between Lower Austria and Burgenland, were used as starting point (Sedy et al. 2022; EEA and Jurečka 2023). These corridors were designed with the aid of geographic information systems. Factors such as land cover, altitude, slope, presence of watercourses, presence of wildlife crossing structures, buildings, road and railway networks were taken into account. Two input layers were modelled: i) the extent of core areas (including stepping stones), and ii) the surface resistance in terms of wildlife migration, both provided the basic framework for modelling the route of ecological corridors in the pilot areas (Plutzar and Sedy 2021a, 2021b). Core areas can be understood as areas that provide long-term

suitable habitat for wildlife, whereas stepping stones are small patches of habitat in the landscape that provide rest and shelter during wildlife migration. Surface resistance refers to the degree of obstacles that wild animals have to overcome during their migration in a fragmented landscape. The ecological corridor model was created using habitat connectivity analysis and the tool Linkage Mapper (McRae and Kavanagh 2011). The first pilot area was located west of the provincial capital city of Linz in Upper Austria (Kobernausser Forest Pilot Area, hereafter KF). The KF landscape (approx. 5 000 km^2) presents itself as a hilly area divided by shallow, mostly unobstructed stream valleys and mainly covered by spruce forests. The second pilot area (Pöttsching Pilot Area, after the nearby municipality, hereafter PÖ) was located south of Vienna in the border area between Lower Austria and Burgenland. From a morphological viewpoint, PÖ (approx. 1 200 km^2) is largely located in a flat or undulating hill country at the edge of the Pannonian Plain. Both pilot areas are embedded in highly human-fragmented landscapes and at the same time are part of important international migration corridors for wildlife (Fig. 1). KF covers parts of an important migration corridor from southern Bohemia to the Central Alps (Bohemian Forest-Northern Alps corridor), while PÖ lies in the Alpine-Carpathian corridor (Birngruber et al. 2012; BMK and EAA 2023). Both areas represent critical sections or bottlenecks along these international corridors (Woess et al. 2002; Birngruber et al. 2012) and are essential in terms of maintaining connectivity in the landscape and permeability for wildlife on the local, supraregional and transnational level.

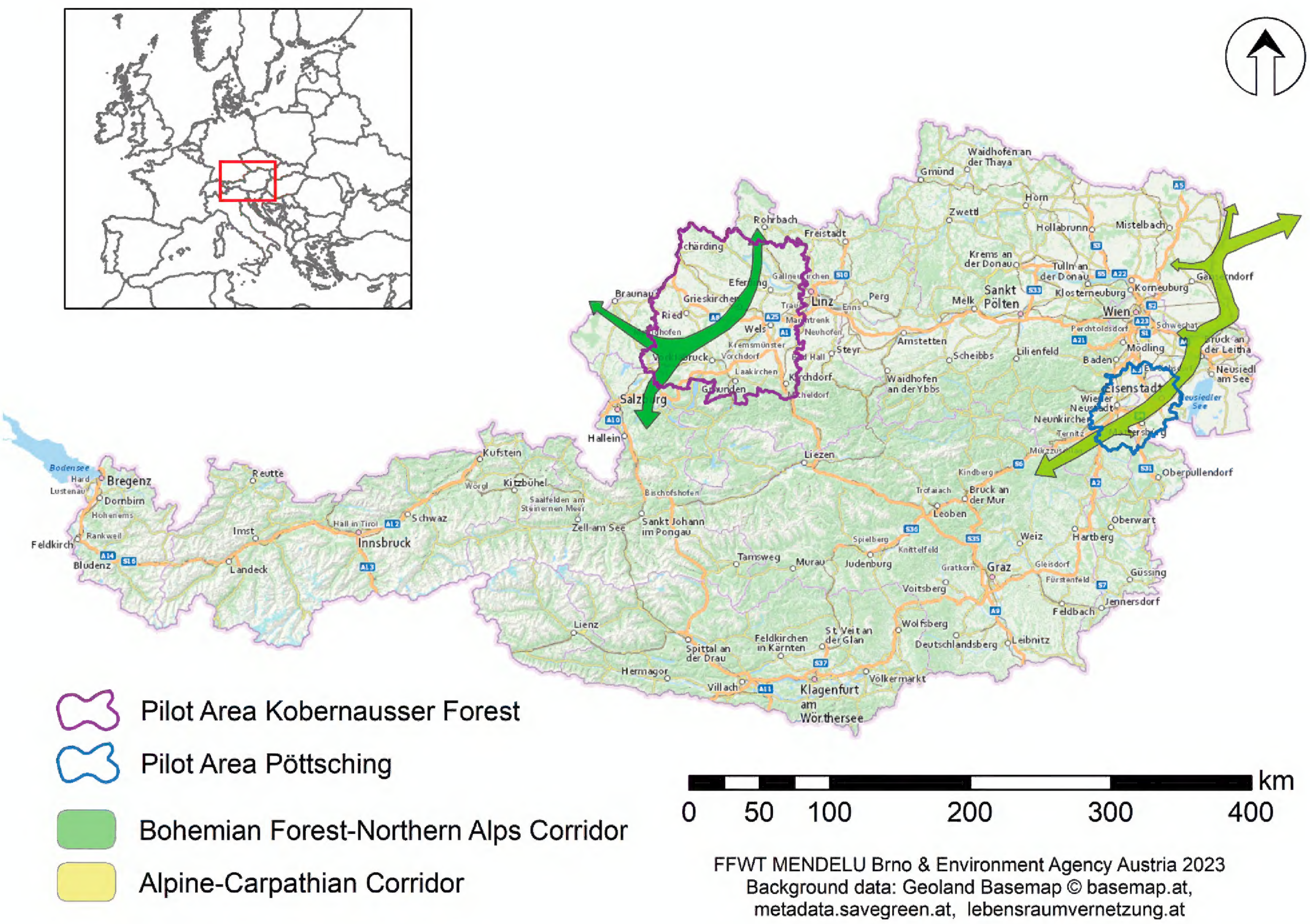

Figure 1. Location of the two pilot areas in Austria and indicative routes of important migration corridors with international connections.

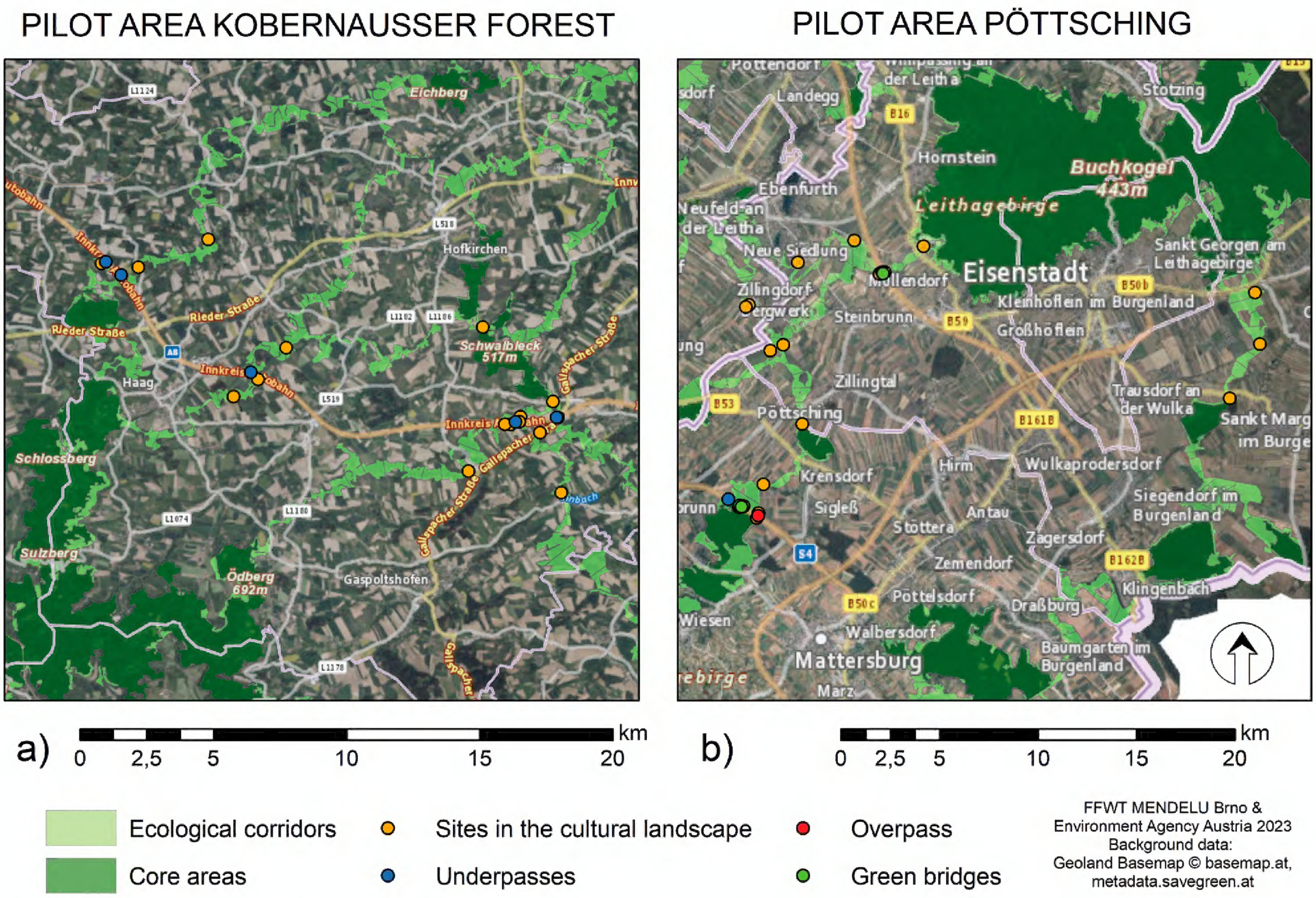

Figure 2. Location of sites with long-term monitoring by camera traps along ecological corridors and on wildlife crossing structures (EEA and Jurečka 2023).

b) Ecological corridors: monitoring sites

We selected a total of 49 sites along ecological corridors incl. WCSs for long-term monitoring, i.e. 21 sites at KF (Fig. 2a) and 28 sites at PÖ (Fig. 2b). The term "site/s" refers to the place and its immediate surroundings where the monitoring was conducted (Fig. 3). All sites were selected on the results of the GIS corridor modelling as part of the SaveGREEN project, the presence of wildlife tracks and routes, and also in coordination with, and in consent with, stakeholders (landowners, hunting associations, land users, mayors, etc.). Each site was provided with an information plate about the ongoing research and contact details. Nine wildlife crossing structures were monitored along the intersection of ecological corridors with motorways and expressways, including 5 underpasses in KF and 2 green bridges (GB), 1 underpass (U) and 1 grey overpass (O) in PÖ (Table 1). The underpasses were featured with asphalt roads and paved surfaces (may therefore be considered as grey underpasses). The grey overpass was equipped with asphalt roads complemented by guardrails and the green bridges were covered with natural surfaces and vegetation. One camera trap was used at each site. A larger number of camera traps were used at green bridges and the underpass due to the representative coverage of the object. Each green bridge was covered by 4 monitoring sites, one underpass (U5) by 2 monitoring sites. For further processing these sites were merged and thereby only one object representing the WCS was used in the analyses. The other 33 sites were located in the cultural landscape. For long-term monitoring, automatic camera traps "COOLIFE Wildlife Camera" were

used. Monitoring took place from 16 December 2021 to 16 January 2023 for the KF and from 2 December 2021 to 28 January 2023 for the PÖ. Central European Time was used uniformly throughout the monitoring period. Camera traps were inspected every 4 to 8 weeks and data downloaded. By using ExifPro 2.1 software, the data was manually sorted by wildlife species or human activity (8 categories, i.e. pedestrians, pedestrians with dogs, cars, agricultural and forestry machinery, cyclists, motorcyclists, horse riders and others), abundance (number of individuals per record), site identification, time and date. For the subsequent objective evaluation of each site, the operating days of each camera traps were recorded. The monitoring methodology focussed specifically on mammals. Individual mammals that could not be determined directly to species were determined only at the genus level. Whereas mammals that remained unidentifiable were included in the special category "undetermined". Regarding the analysis of the relationship of the effect of human frequency on the number of mammal crossings in WCSs, data on human activities obtained from records for the majority of WCSs was used, however only for the underpass U5, traffic count data was used, i.e. 4,533 vehicles per day, annual average daily traffic of the year 2022 (DORIS 2023). A total of 56,717 mammal and human relevant records were obtained during the monitoring period, divided into 28,128 records from KF and 28,589 records from PÖ.

Table 1. Monitored wildlife crossing structures.

ID	Type WCS	Name	GPS coordinates (WGS84)	Road ID	Width of WCSs (m)	Pilot area
U1	Underpass	Straß	48°12'52.4"N, 13°37'31.6"E	A8	6	KF
U2	Underpass	Renhartsberg	48°12'40.6"N, 13°37'48.2"E	A8	5	KF
U3	Underpass	Rampersdorf	48°11'21.7"N, 13°40'26.0"E	A8	6	KF
U4	Underpass	Thalheim	48°10'41.3"N, 13°45'48.3"E	A8	8	KF
U5	Underpass	Niederetnisch	48°10'45.2"N, 13°46'38.7"E	A8	40	KF
U6	Underpass	Bad Sauerbrunn	47°46'44.8"N, 16°21'33.6"E	S4	70	PÖ
O	Overpass	Sigleß	47°46'26.1"N, 16°22'22.6"E	S4	7	PÖ
GB1	Green bridge	Pöttsching	47°46'37.3"N, 16°21'53.9"E	S4	80	PÖ
GB2	Green bridge	Müllendorf	47°50'55.4"N, 16°25'47.1"E	A3	50	PÖ

Note: The width of the WCSs was measured parallel to the intersecting road and was measured approximately using GIS (using orthophotos). WCSs were named after the nearest municipality.

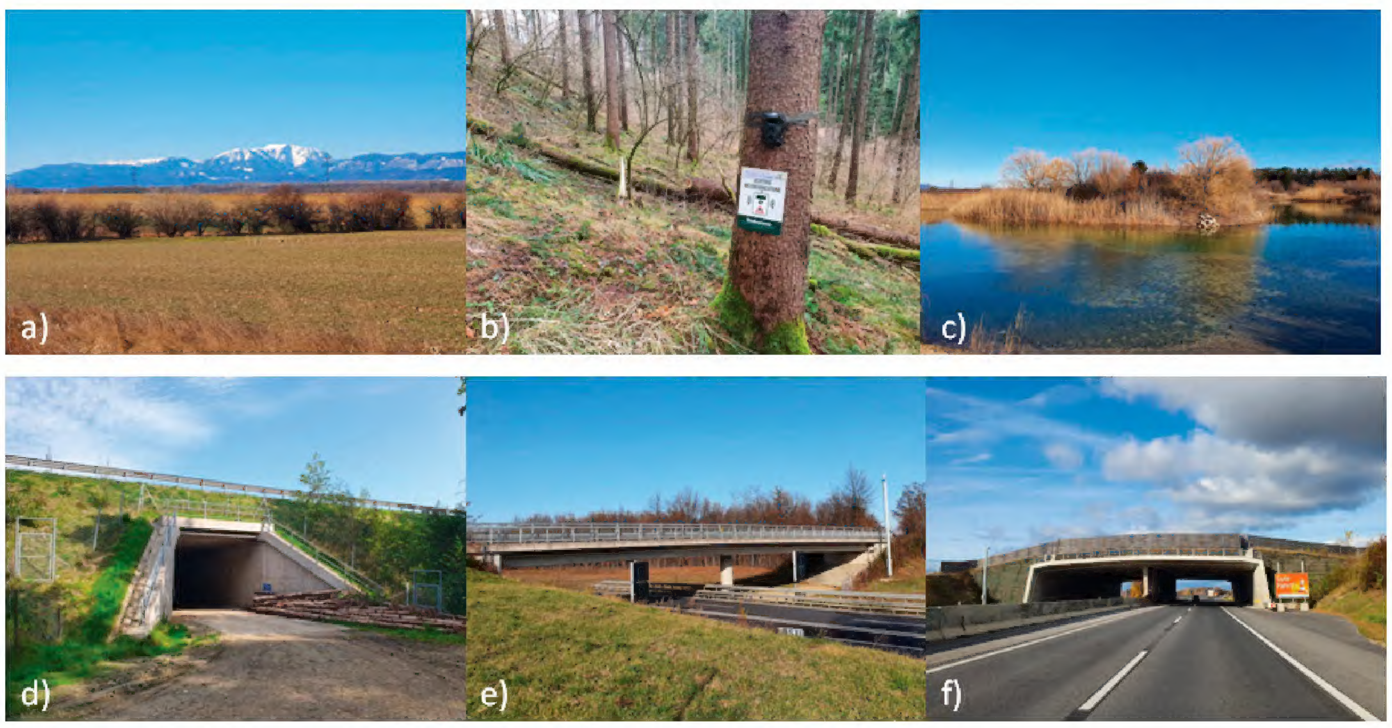

Figure 3. Monitoring sites along ecological corridors incl. WCSs: sites in the cultural landscape **a** farmland in PÖ **b** forest habitat in KF **c** standing water in PÖ **d** underpass (U1) of the A8 Innkreis motorway **e** grey overpass (O) over the S4 Mattersburger expressway **f** green bridge (GB2) near Müllendorf over the A3 Südost motorway (photos: Mořic Jurečka).

c) Ecological corridors: descriptive variables

For the spatial assessment and map output, the landcover layer EUNIS Biotoptypen Österreichs 2018 (EEA 2023) and additionally road infrastructure, watercourses, water bodies (data.gv.at 2023; geoland.at 2023), core areas and ecological corridors (EEA and Jurečka 2023) were used. Spatial data was processed with ArcMap 10.4.1. (ESRI 2015) using the ETRS 1989 LAEA coordinate system for reasons of suitability for the territory of Austria. To determine the degree of ecological stability and the degree of human disturbance in the vicinity of the monitoring sites, information on landcover (habitat types EUNIS 2018) in a circular buffer was used to evaluate the CES (Míchal 1982; Löw 1995; Chromčák et al. 2021). A diameter 1000 m was chosen with respect to the width of corridors of international importance and as recommended for international corridors in Upper Austria (Birngruber et al. 2012). The coefficient of ecological stability (CES) shows the ratio of relatively stable (S) to relatively unstable (UN) areas in a particular area, represented by the following expression:

$$CES = \frac{S}{UN} = \frac{X + F + E + G + C}{J + I}$$

To calculate the CES value via layer land cover (Table 2), the CES formula was used for each locality and the methodology of the Czech Statistical Office (Table 3) was used to interpret the results (Czech Statistical Office 2023). Euclidean distances were used to determine the proximity between monitoring sites and landscape features with potential impacts on mammals.

Table 2. Legend of relevant layers of EUNIS 2018 habitat types (EEA 2023) used for the analyses of CES.

Layer ID	Description of EUNIS habitat types
J	Constructed, industrial and other artificial habitats
I	Regularly or recently cultivated agricultural, horticultural and domestic habitats
X	Habitat complexes
F	Heathland, scrub and tundra
E	Grasslands and lands dominated by forbs, mosses or lichens
G	Woodland, forest and other wooded land
C	Inland surface waters

Table 3. Possible interpretation of the CES (Czech Statistical Office 2023).

CES value	Explanation
CES < 0.10	areas with maximum disturbance of natural structures
0.10 < CES < 0.30	areas with above-average use, with clear disturbance of natural structures
0.30 < CES < 1.00	areas intensively exploited, especially by large-scale agricultural production, weakening of autoregulatory processes in ecosystems
1.00 < CES < 3.00	areas with a broadly balanced landscape in which human influence is relatively consistent with preserved natural structures
CES > 3.00	areas with natural and close to nature landscapes with a significant predominance of ecologically stable structures and low intensity of human use of the landscape

d) Statistical analysis

In order to scrutinize the relationship between wildlife activities and the characteristics of the surroundings of the WCS, the recorded mammal data obtained from terrestrial monitoring at each site and the outputs from the spatial analysis were statistically compared using R software (R Core Team 2022). The processing was carried out using data on CES values, distances (abbreviated: DIST) from landscape features, the number of species at the sites and the average daily activity (hereafter ADA) of mammals at the site (average of total mammal records at the site to the number of operation days of the camera trap) and selected large mammal species (red deer, wild boar, roe deer). These were selected as representative species given their habitat requirements according to the proposed aspects of the ecological corridors (Plutzar and Sedy 2021a, 2021b) as well as potential risk and damage of wildlife-vehicle collisions. In treating the effect of distance from the motorways incl. expressways, only sites along ecological corridors outside of wildlife crossing structures were processed.

The software R (R Core Team 2022) was used to create scatterplots, correlation diagrams as well as other graphs and served for statistical testing. A linear regression (represented by a red line) has been fitted to the scatterplots. Spearman's correlation coefficient (r) was used to test and evaluate the relationship between the number of species and their activity in relation to landscape features, CES value, human activity and WCSs width. Mammals ADA with respect to the type of WCS was compared by applying the two-sample Wilcoxon rank sum test (Hollander and Wolfe 1973).

Results

a) Descriptive analysis: mammals

A total of 18 mammal species was recorded on the ecological corridors including WCSs during the monitoring period (Table 4). The highest number of species was found in the PÖ (16 species compared to 10 species in the KF). The most abundant mammal was roe deer (*Capreolus capreolus*) (51.24%), followed by European hare (*Lepus europaeus*) (20.51%) and wild boar (*Sus scrofa*) (8.39%). In contrast, the least abundant mammals registered were European beaver (*Castor fiber*), hedgehog (*Erinaceus* spp.), European rabbit (*Oryctolagus cuniculus*), European otter (*Lutra lutra*), European wildcat (*Felis silvestris*), least weasel (*Mustela nivalis*), European fallow deer (*Dama dama*), European mouflon (*Ovis aries musimon*), red deer (*Cervus elaphus*) and golden jackal (*Canis aureus*). European beaver, European muflon, European otter, European rabbit, European fallow deer, golden jackal, least weasel and red deer were recorded only in PÖ whereas wildcat and hedgehog were recorded exclusively in KF. The majority of records have been obtained on ecological corridor sites in the cultural landscape (61.05%) compared to WCSs (38.95%).

Table 4. Mammal presence in pilot areas on ecological corridors incl. WCSs.

Species	KF		PÖ	
	n	%	n	%
domestic cat (*Felis catus*)	1924	13.93	103	0.46
European badger (*Meles meles*)	64	0.46	213	0.95
European beaver (*Castor fiber*)	–	–	49	0.22
European hare (*Lepus europaeus*)	3180	23.02	4253	18.96
European mouflon (*Ovis aries musimon*)	–	–	203	0.91
European otter (*Lutra lutra*)	–	–	6	0.03
European rabbit (*Oryctolagus cuniculus*)	–	–	13	0.06
European wildcat (*Felis silvestris*)	3	0.02	–	–
European fallow deer (*Dama dama*)	–	–	2	0.01
golden jackal (*Canis aureus*)	–	–	1	0.01
hedgehog (*Erinaceus* sp.)	40	0.29	–	–
least weasel (*Mustela nivalis*)	–	–	3	0.01
marten (*Martes* sp.)	549	3.97	822	3.66
red deer (*Cervus elaphus*)	–	–	699	3.12
red fox (*Vulpes vulpes*)	390	2.82	1566	6.98
red squirrel (*Sciurus vulgaris*)	155	1.12	208	0.93
roe deer (*Capreolus capreolus*)	7487	54.20	11085	49.42
wild boar (*Sus scrofa*)	3	0.02	3039	13.55
undetermined	18	0.13	165	0.74

b) Descriptive analysis: humans

The number of records of human activities in KF was almost twice as large compared to PÖ (Table 5). Overall, cars were more than half as represented (53.72%), followed by human activity categories such as pedestrians (17.54%), agricultural and forestry machinery (11.66%), cyclists (7.84%), pedestrians with dogs (5.51%), motorcyclists (1.62%), other categories (1.28%) and horse riders (0.84%).

Table 5. Human presence in pilot areas along ecological corridors incl. WCSs.

Human activity	KF		PÖ	
	n	%	n	%
agricultural and forestry machinery	1624	10.17	1302	14.27
cars	10111	63.34	3365	36.88
cyclists	1201	7.52	765	8.38
horse riders	8	0.05	202	2.21
motorcyclists	235	1.47	171	1.87
others (excavators, trucks, etc.)	258	1.62	62	0.68
pedestrians	1946	12.19	2454	26.89
pedestrians with dogs	579	3.63	804	8.81

c) Patterns of mammal and human activity

Mammal activity was recorded mainly during the night hours. Throughout the year increased levels of activity of mammals was observed during dawn and dusk (Fig. 4). The highest frequency of activity of mammals was recorded in spring months. Human activity was recorded mainly during day for the entire year (Fig. 5). Human activity was predominant in the morning and afternoon hours. However, a decrease in human activity was recorded, especially in the midday hours throughout the year.

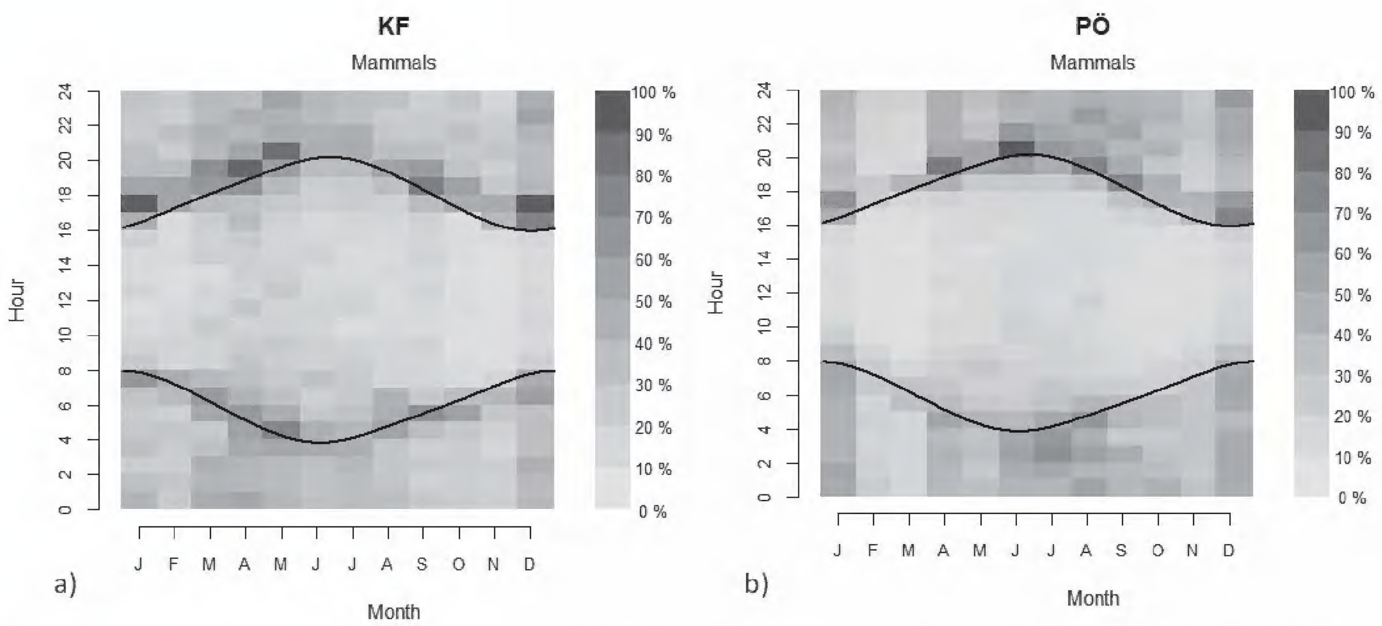

Figure 4. Annual and daily time distribution of mammal activity in KF (**a**) and PÖ (**b**). The solid black line represents the sunrise and sunset times during the year.

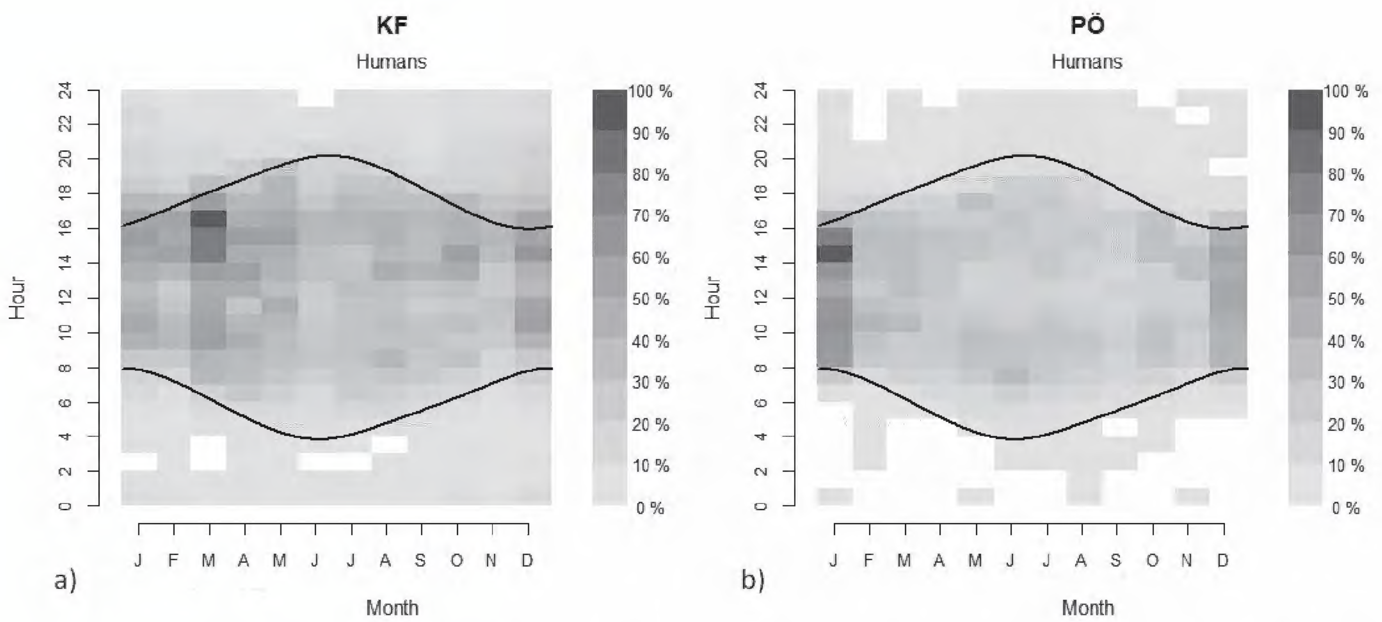

Figure 5. Annual and daily time distribution of human activity in KF (**a**) and PÖ (**b**). The solid black line represents the sunrise and sunset times during the year.

d) Coefficient of ecological stability

Almost 80% of all monitored sites on ecological corridors showed a CES value less than 1, indicating that these areas are characterised by disturbed natural structures and intensive human use (Fig. 6).

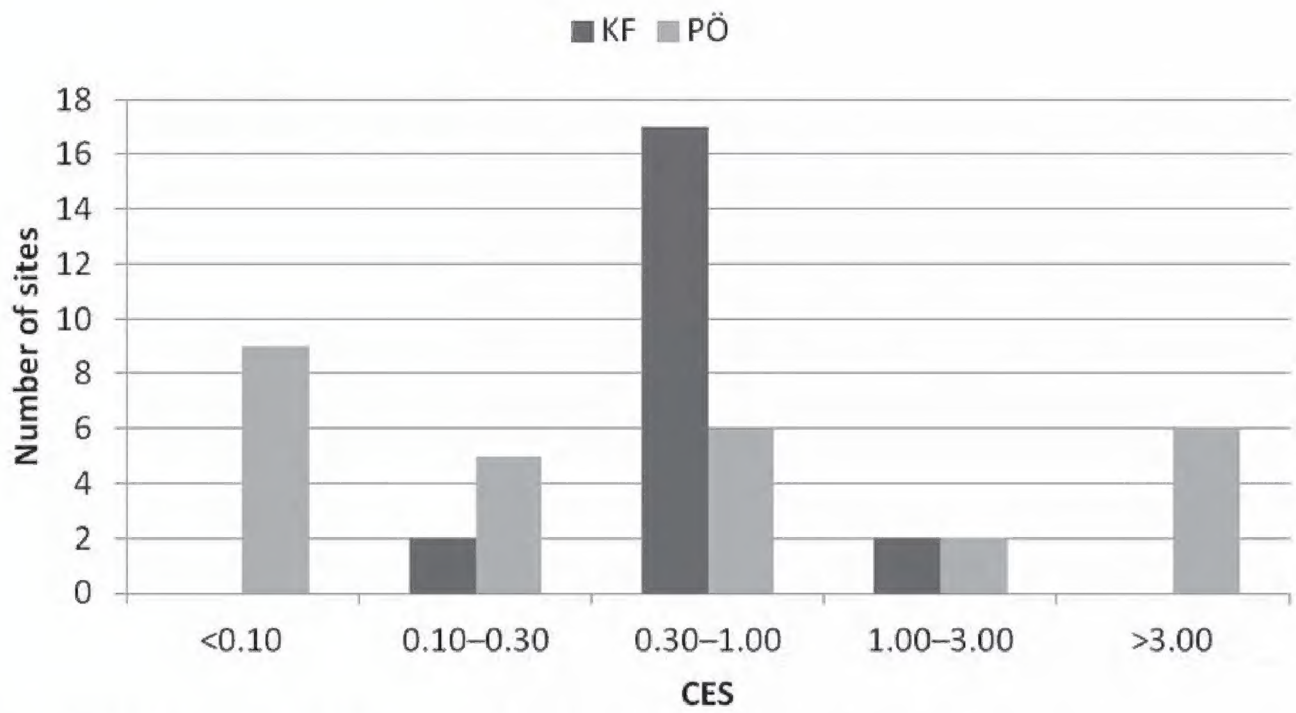

Figure 6. Coefficient of Ecological Stability (CES) values by pilot area monitoring sites.

A positive correlation (r = 0.29, p-value = 0.0471) was found between the number of species recorded and the CES value (Fig. 7a). Furthermore, a positive correlation (r = 0.26, p-value = 0.0689) was also observed with the ADA of mammals and the CES value (Fig. 7b).

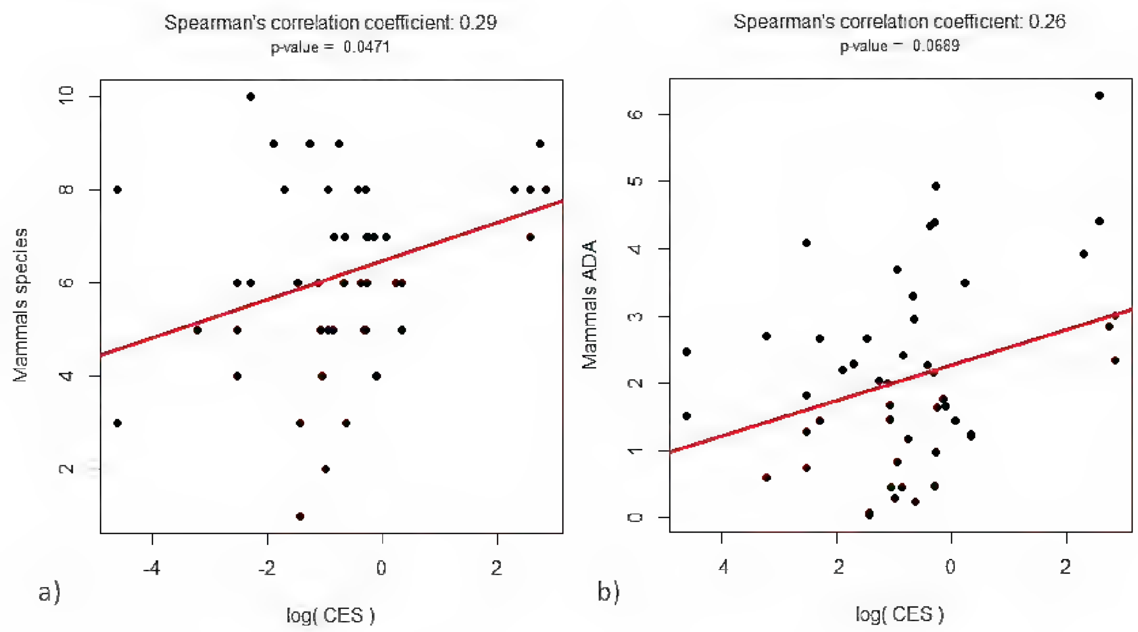

Figure 7. a Relationship between the number of species and **b** average daily activity (ADA) of mammals, and the logarithm of the ecological stability coefficient (CES), linear regression is shown in red.

e) Landscape features

The relationship of mammal presence as well as mammal activity and selected landscape features is presented in a correlation matrix (Fig. 8). Strong correlations were found between some related environmental parameters, for example between distance from built-up areas and distance from motorways. The strongest significant positive correlation with CES value was observed for ADA of red deer. The strong significant negative correlation with the CES value was observed for distance from core areas and also distance from forests.

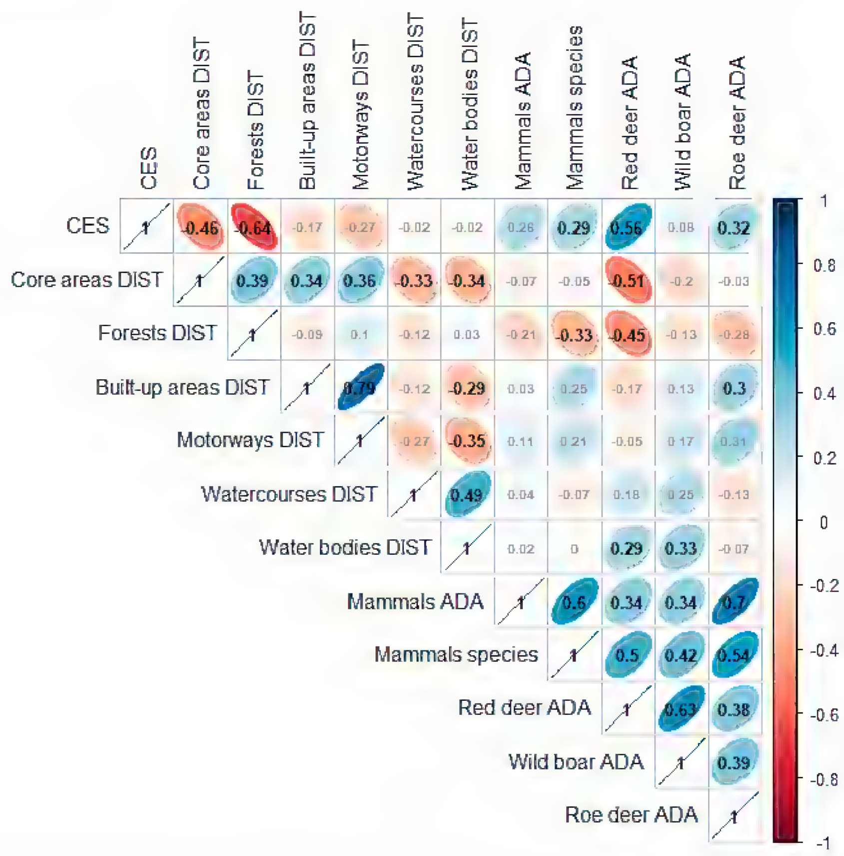

Figure 8. Multi-factor correlation matrix (CES, DIST: distance, ADA: average daily activity). Significant correlation coefficients (at significance level of 5%) are displayed in black while non-significant coefficients are presented in grey. The right side of the figure shows a scale for the correlation coefficient r indicating the colour codes used.

The average daily activity of red deer was influenced by environmental parameters. Significant negative correlations with red deer ADA were found for distance from core areas and forests, significant positive correlations were found for CES and distance from water bodies. The average wild boar daily activity was significantly positively correlated with distance from water bodies. The wild boar daily activity significantly positively correlated with red deer activity and activity of all mammals. The average roe deer daily activity was significantly positively related to CES and distance from built-up areas. The daily activity of roe deer was significantly positively correlated with red deer and wild boar activities, as well as with activity of all mammals combined.

f) Wildlife crossings structures

Altogether, 11 species were identified at the investigated WCSs (Table 6). The highest number of species was recorded on the green bridges (GB1, GB2) and at the U1 underpass. Average daily mammal activity at the green bridges is about 12.45 crossings per day (n = 2), approx. 3 times more than at the surveyed overpass (n = 1) and approx. 6 times more than the average daily mammal activity at all surveyed underpasses (n = 6). The highest number of species and the highest level of daily activity was recorded on the green bridge GB1 near Pöttsching, whereas the lowest number of species and the lowest daily activity was recorded on the underpass U5 near the residential area Niederetnisch. Only domestic cat

Table 6. Mammal and human presence in WCSs.

	U1		U2		U3		U4		U5		U6		O		GB1		GB2	
	n	*ADA*	*n*	*ADA*	*n*	*ADA*	*n*	*ADA*	*n*	*ADA*	*n*	*ADA*	*n*	*ADA*	*n*	*ADA*	*n*	*ADA*
domestic cat (*Felis catus*)	178	0.48	142	0.36	838	2.55	395	1.04	21	0.07	10	0.02	18	0.26	14	0.04	5	0.01
European badger (*Meles meles*)	–	–	–	–	–	–	–	–	–	–	–	–	2	0.03	37	0.10	75	0.25
European hare (*Lepus europaeus*)	143	0.38	154	0.39	457	1.39	230	0.60	2	0.01	67	0.16	32	0.47	526	1.46	1640	4.38
golden jackal (*Canis aureus*)	–	–	–	–	–	–	–	–	–	–	–	–	1	0.01	–	–	–	–
hedgehog (*Erinaceus* spp.)	7	0.02	–	–	–	–	24	0.06	–	–	–	–	–	–	–	–	–	–
marten (*Martes* spp.)	34	0.09	8	0.02	66	0.20	32	0.08	9	0.05	–	–	222	3.26	53	0.15	37	0.10
red deer (*Cervus elaphus*)	–	–	–	–	–	–	–	–	–	–	4	0.01	–	–	515	1.36	–	–
red fox (*Vulpes vulpes*)	5	0.01	259	0.66	18	0.05	17	0.04	–	–	20	0.05	20	0.29	209	0.57	323	0.85
red squirrel (*Sciurus vulgaris*)	1	0.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
roe deer (*Capreolus capreolus*)	527	1.42	290	0.73	238	0.73	69	0.18	–	–	382	0.93	–	–	3304	9.07	800	2.29
wild boar (*Sus scrofa*)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1499	3.97	4	0.01
undetermined	7	0.02	2	0.01	–	–	–	–	–	–	13	0.03	–	–	94	0.25	16	0.04
Total mammal activity	**902**	**2.42**	**855**	**2.16**	**1617**	**4.93**	**767**	**2.01**	**32**	**0.13**	**496**	**1.21**	**295**	**4.34**	**6251**	**16.97**	**2900**	**7.94**
Species richness	7	–	5	–	5	–	6	–	3	–	5	–	6	–	8	–	7	–
agricultural and forestry machinery	47	0.13	247	0.63	683	2.08	456	1.20	–	–	952	2.32	189	2.78	–	–	1	0.00
cars	373	1.00	169	0.43	1126	3.43	8259	21.68	*	4533	3046	7.43	312	4.59	–	–	–	–
cyclists	52	0.14	–	–	10	0.03	1117	2.93	–	–	690	1.68	37	0.54	–	–	34	0.10
horse riders	1	0.00	–	–	–	–	2	0.01	–	–	173	0.42	13	0.19	–	–	16	0.05
motorcyclists	6	0.02	–	–	22	0.07	176	0.46	–	–	151	0.37	1	0.01	–	–	3	0.01
others (excavators, trucks, etc.)	75	0.20	75	0.19	7	0.02	101	0.27	–	–	47	0.11	2	0.03	–	–	1	0.00
pedestrians	213	0.57	164	0.42	98	0.30	930	2.44	2	0.01	1576	3.84	276	4.06	135	0.39	183	0.49
pedestrians with dogs	8	0.02	18	0.05	121	0.37	348	0.91	–	–	535	1.30	62	0.91	18	0.05	54	0.16
Total human activity	**775**	**2.08**	**673**	**1.70**	**2067**	**6.30**	**11389**	**29.89**	**2**	**4533**	**7170**	**17.49**	**892**	**13.12**	**153**	**0.44**	**292**	**0.82**

Note: ADA – average daily activity in this regard refers to the average daily crossings of a species, * – traffic count data was used (DORIS 2023).

and hare were recorded on all WCSs surveyed. Smaller mammals such as squirrel and hedgehog were only recorded at the underpasses. A rare record of a golden jackal was observed on the grey overpass in the PÖ. Large mammals such as red deer and wild boar clearly preferred, in terms of mammals ADA, the green bridges compared to the underpasses and grey overpasses examined (p-value = 0.0278, one-sided Wilcoxon rank sum test). Red deer were occasionally recorded at the nearby underpass, however the majority of crossings were recorded on the green bridge GB1 (99.23% of all records). The highest average human activity per day was observed at the U4, U5 and U6 underpasses, while the lowest mean values were recorded at green bridges GB1 and GB2.

A positive correlation was noted between the width of WCSs and the number of species as well as the ADA of mammals; no relationship was observed for the width of WCSs and the average daily human activity (Fig. 9). These three correlation coefficients were statistically insignificant. A significant negative correlation was found between the average daily human activity on WCSs and (i) the number of species (r = -0.68, p-value = 0.0422), and (ii) the ADA of mammals (r = -0.83, p-value = 0.0083). Green bridges displayed the highest wildlife activity and the lowest human activity compared to the other types of WCSs (Table 6).

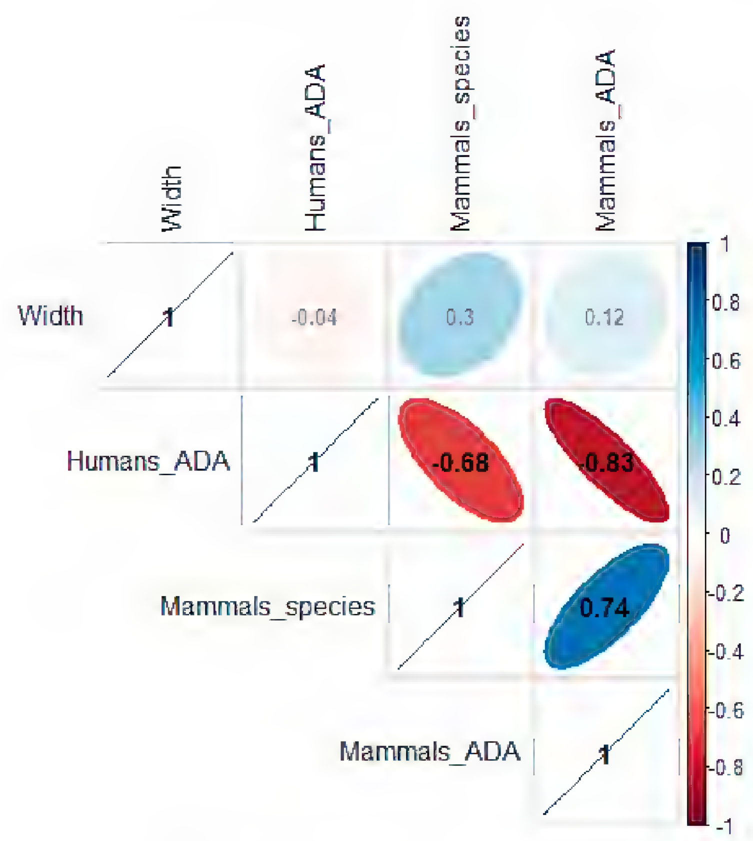

Figure 9. Correlation matrix of selected factors influencing the effectiveness of WCSs. Significant correlation coefficients (on the significance level of 5%) are displayed in black while non-significant coefficients are presented in grey. The right side of the figure shows a scale for the correlation coefficient r with the colour codes used.

Discussion

a) Wildlife monitoring at sites on ecological corridors and time variation

Maintaining structural and functional connectivity is crucial for the long-term sustainability and viability of wildlife populations as well as for safeguarding ecosystem functions in human-altered landscapes. Ecological corridors are serving the goal of maintaining connectivity in the landscape. The selected monitoring locations were chosen based on the given requirements and limitations, primarily caused by the willingness of landowners and land users, as well as by the corridor routes defined initially. To optimise coverage, it would

be advisable to monitor the ecological corridors even more comprehensively using additional monitoring sites, in particular to compare the sites with regard to the occurrence of wildlife in the core areas.

The highest species richness was recorded in the pilot area Pöttsching (PÖ) compared to the pilot area Kobernausser forest (KF). The abundant species richness in the PÖ may be related to local conditions at the interface of three different biogeographical regions, i.e. the Alpine, Continental and Pannonian regions (EEA 2017) and due to its location on the Alpine-Carpathian corridor (BMK and EAA 2023). It is important to emphasise that not all species of mammals were recorded consistently at every location on the ecological corridors incl. wildlife crossings structures (WCSs). This may be related to the current degree of anthropogenic fragmentation of habitats in the pilot areas, which may be particularly problematic for sensitive species and large mammals such as red deer, wild boar or large carnivores. Motorways represent a significant genetic barrier for red deer, which, in contrast, does not apply to wild boar (Frantz et al. 2012). For example, red deer was recorded only in PÖ while wild boar was recorded in both pilot areas. Red deer were found near the core areas and forests, e.g. near and south of the GB1 green bridge (Rosalia Mountains), north of the municipality of Müllendorf (Leitha Mountains) or in the vicinity of the municipality of Sankt Margarethen in Burgenland. However, they could practically not be found in locations along the ecological corridors between these core habitats. Only in the vicinity of the core areas (Rosalia, Leitha Mountains) European mouflon and fallow deer were recorded as well, while no evidence was recorded in between those areas. In contrast, wild boar was recorded at almost all of the monitored sites in PÖ, but compared to KF, it was recorded at only two sites north of the A8 motorway and did not cross any monitored WCSs. In this context, it must be taken into account that ungulate populations and associated occurrence may be significantly influenced by hunting management. Large carnivores such as the grey wolf and the Eurasian lynx were not recorded as part of our monitoring. This may be due to the fact that the investigated pilot areas are already significantly fragmented and disturbed by humans, which represents a major problem for large mammals, causing them to seek other, less disturbed routes. Although there were occasional reports of observations of grey wolves and lynx in the vicinity of the pilot areas, they were not observed along the designated ecological corridors as part of this work (Birngruber et al. 2012; Kora 2023; Marucco et al. 2023). This is in line with Ripari et al. (2022) suggesting that human disturbance is a limiting factor for habitat selection of large carnivores in continental Europe. Human disturbance may not be the main problem - in the case of wolves, for example, genetic studies confirm their migrations of several hundred kilometres across densely populated parts of Europe (Andersen et al. 2015; Hindrikson et al. 2017). Another factor that noticeably affects the spread and recovery of wildlife populations, especially large carnivores, which must be taken into account, is hunting and illegal killing (Kaczensky et al. 2011). The known spread of the golden jackal in Europe (Spassov and Acosta-Pankov 2019; Frangini et al. 2022) was also substantiated by our study with one record on a grey overpass (O) near the municipality of Sigleß. It is unclear whether it was a local individual, e.g. from the area of Lake Neusiedl, where the first breeding of the golden jackal in Austria was described (Herzig-Straschil 2007), or a migrating individual from the Pannonian Plain or South-Eastern

Europe (Lanszki et al. 2006; Hatlauf et al. 2017; Spassov and Acosta-Pankov 2019). Furthermore, a rare occurrence of European wildcat was observed in the KF pilot area (near the municipality of Haag am Hausruck), which would be consistent with relevant studies (Friembichler and Slotta-Bachmayr 2013; Slotta-Bachmayr et al. 2017), which indicates a relatively suitable habitat and refers to historical records of occurrence in this area. In order to objectively verify the presence of European wildcat, genetic analysis would be necessary, to confirm or completely exclude whether it was an individual of a domestic cat or a hybrid (Pierpaoli et al. 2003; Slotta-Bachmayr et al. 2017). In the Wachau region (east-oriented from KF), a small breeding population of European wildcat was recently confirmed by genetic analysis (Gerngross et al. 2021), which supports the assumption of migrating individuals. Furthermore, semi-aquatic species such as European otter and European beaver were recorded only in PÖ at locations near water courses (near the municipality of Oslip). The European beaver probably spread from the Danube River or the Pannonian Plain, and is expected to increase in population size (Halley et al. 2021). Although the European otter was documented in almost the entire territory of Austria (Kranz and Poledník 2020), in our case only isolated occurrence records were registered, which may indicate a fragmented distribution. Moreover semi-aquatic species are difficult to monitor due to their specific habitat conditions (Mata et al. 2005) and could therefore be underrepresented. Species such as roe deer, brown hare, marten, European badger, domestic cats, red fox and squirrel, which are usually common in human-modified landscapes, were also abundantly recorded. For roe deer, an increase in population size is generally observed, which refers to its good adaptation to human-dominated landscapes and is also consistent with its high ranking among the most frequent victims of wildlife-vehicle collisions (Ignatavičius et al. 2020; Bíl et al. 2023). Some species of particularly small and medium-sized mammals may not have been recorded at every site due to the technical limitations of camera traps (Jumeau et al. 2017). The higher number of domestic cats recorded in KF should be emphasised, which is probably related to human presence and scattered built-up areas in the landscape.

Most mammal records were registered at night with a significant increase in activity around dawn and dusk. This general trend is consistent with a number of studies and corresponds to the high probability of collision between wild animals and vehicles at dawn and dusk (Morelle et al. 2013; Krukowicz et al. 2022). The peak activity of mammals during the year was recorded in spring, followed by summer and during the transition from autumn to winter. This is also supported by trends in wildlife-vehicle collisions recorded in other studies (Krukowicz et al. 2022; Bíl et al. 2023). Human activity was recorded mainly during the day and characterised by two peaks (in the morning and in the afternoon), which is also supported by various studies (Reilly et al. 2017; Lewis et al. 2021). Increased human activity in the afternoon is also reflected in human-caused traffic accidents (Krukowicz et al. 2022). The peak in human activity was recorded in spring and subsequently decreased, which is probably related to the increase in the frequency of agricultural management measures, or other activities conducted in the landscape. The categories of human activity were represented relatively balanced across the pilot areas. However, KF was clearly dominated by activities associated with the use of cars, which may have been influenced by the number of underpasses in KF.

b) The influence of the coefficient of ecological stability, vegetation cover and landscape features

In our study the ecological stability coefficient (CES), which is used to express ecological stability under human influence at regional scale (Chromčák et al. 2021) illustrates the characteristics of the surrounding area of the monitoring sites and its impact on mammals occurrence on ecological corridors. Furthermore, additional information of important landscape elements that potentially have influence on the occurrence of mammals were considered. The quality of the results of the GIS-based calculations of the CES values and the distances from landscape elements was probably influenced by the quality of the background data used, especially regarding spatial accuracy and actuality. Data used as the basis for the calculations of the CES relate to 2018 while field work was carried out from 2021 to 2023. This discrepancy may have an influence on the results.

The results suggest that ecological corridors can fulfil their function and ensure the movement of mammals (Table 4) even in human-modified landscapes such as those found in the regions (Fig. 6). CES emphasises areas that are stable in an ecological context such as grasslands, shrubs, scattered vegetation, woodlands, forests and habitat complexes. The results indicate that various types of vegetation and habitat structures can noticeably support the activity and migration of species, and in the case of mammals also lead to increased species richness. This is supported by the negative relationship between the number of species and the activity of mammals, especially when considering large mammals such as red deer, and the distance from core areas and forest complexes. These results emphasise the importance of ecological restoration of such landscapes, for example through enrichment with landscape structures along ecological corridors. Especially in the context of rural agricultural landscapes, the implementation of the concept of green infrastructure (GI) as a strategically planned network of natural and semi-natural areas could significantly improve the permeability of featureless landscapes between core areas. Studies therefore argue for the development of customised local GI maps to highlight local requirements and options for such GI and to provide decision support for investment in GI, since the visualisation of priority conservation areas in a spatially explicit manner could support decision-makers to optimally allocate limited resources for ecosystem conservation and restoration (Danzinger et al. 2021). Ecological corridors would benefit from different zones of protection with customised degrees of applied management. Therefore applied management such as using zones of continuous canopy vegetation together with a buffer zone of scattered vegetation with grass cover, is highly recommended. The use of agroforestry systems, i.e. the integration of trees and shrubs into farming practices, and the restoration of elements of GI in the vicinity of ecological corridors would also be suitable for promoting biodiversity and wildlife connectivity (Jose 2012; Dondina et al. 2019; Udawatta et al. 2019). Moreover, the use of additional GI elements such as hedges and small woody features can increase ecological stability in the landscape while combining productive and protective functions for agricultural landscapes. Depending on the particular species, each measure can naturally entail a number of restrictions, which makes cross-species consideration essential for the planning

of implementation measures. Although this work has not scrutinized the width of ecological corridors, which is one of the important factors influencing the distribution of species, the use of the guiding principle "the bigger the better" can be recommended (Bond 2003; Samways et al. 2010; Ford et al. 2020).

Furthermore, there was a positive association between the number of species and increasing distance from motorways and built-up areas. This suggests that human presence and associated disturbance affects the distribution of species in the landscape (Barrueto et al. 2014; Dertien et al. 2021). This finding may indicate the influence of the barrier effect (Lodé 2000; Jacobson et al. 2016; Seiler and Bhardwaj 2020). A lower correlation value was recorded for species activities, which is probably related to the disproportion of sites near anthropogenic features or the results may have been biased by synanthropic animals (such as the domestic cat and marten). A positive correlation was observed for roe deer and less positive correlation for wild boar, which is probably related to the ecology of these species. A slightly negative correlation was recorded for red deer, which is certainly influenced by the disproportion of record occurrence and the small sample size. There was almost no relationship between water features (watercourses, water bodies) and species or their average daily activity. This is probably due to the relatively small sample size, which influenced the result regarding the weak dependence on water features for roe deer and the opposite trend for red deer and wild boar.

c) Wildlife crossings structures

In the study, 9 different wildlife crossing structures (WCSs) were monitored, which support the crossing of high-traffic transport infrastructure by the routes of the ecological corridors. The distribution of the number of WCSs types was not ideal in terms of variables and for the subsequent statistical processing. This distribution is probably the reason why no statistically significant correlation was found between the width of the WCSs and efficiency in terms of the number of species crossing and their average daily activity. The importance of not only the width but also other parameters (length, height, openness, slopes) of the WCSs is supported by a number of studies (Van Wieren and Worm 2001; Grilo et al. 2008; Mata et al. 2008; Mysłajek et al. 2020). However, it is also important to consider the shape of the object, material, subsoil, location and many other biotic or abiotic factors (Denneboom et al. 2021; Brennan et al. 2022). The specific demands and responses of each species to the width factor also need to be taken into account (Brennan et al. 2022). Our study identified 11 species on WCSs compared to 18 species on sites in the surrounding cultural landscape. The technical aspects of WCSs (design, size, location and densities of WCSs) may vary depending on the specific location and the particular animal species (small, medium or large fauna). Small fauna species (e.g. reptiles, amphibians, flightless insects) often constitute habitat specialists and therefore the design details and equipment of WCS should always be adapted with respect to the their requirements. For this reason as well as to ensure the maximum efficiency of the WCS for all species and to maintain functional connectivity in the landscape, it is necessary to take into account a number of existing practical guidelines and recommendations for the design and the maintenance of WCSs (Iuell et al. 2003; Van Der Ree et al. 2015a; Hlaváč et al. 2019; Reck et al. 2019, 2023a).

There was a statistically significant negative correlation between ADA of humans and ADA of mammals, including the number of species on WCSs. This indicates that human presence and associated human disturbance in the surrounding environment significantly influences mammal movement across WCSs. This is supported by a number of other studies showing the negative impact of humans on wildlife (Barrueto et al. 2014; Denneboom et al. 2021; Dertien et al. 2021). For this reason, it may be recommended to completely avoid or minimise human activities in and around important WCSs and along ecological corridor routes to ensure better efficiency.

Green bridges (wildlife overpasses) showed better efficiency compared to underpasses or grey overpasses, either in terms of daily crossing rate or total number of observed species. The effectiveness of WCSs in general is influenced by a number of parameters and factors (Mysłajek et al. 2020; Brennan et al. 2022) that have been mentioned above, however, in the case of green bridges the presence of vegetation cover and the possibility of crossing over road infrastructure is an unparalleled advantage in comparison to ordinary bridges (grey overpasses) or underpasses (grey underpasses). The distance to vegetation cover is one of the important factors affecting the passage of large mammals (Clevenger and Waltho 2005). In our case, the effectiveness of green bridges was influenced by lower levels of human activity compared to other types of WCSs. Although other studies show better effectiveness of wildlife overpasses compared to underpasses (Simpson et al. 2016; Mysłajek et al. 2020), there remains a need for all WCSs to meet the goals of mitigating the impacts of habitat fragmentation by restoring connectivity and reducing the risk of wildlife-vehicle collisions to ensure better traffic safety (Olsson et al. 2008; Smith et al. 2015; Simpson et al. 2016). Different species are known to use and have various responses to different types of WCSs (Clevenger and Waltho 2005; Mata et al. 2005), which should be considered when designing WCSs for target species in specific locations (Smith et al. 2015). The results show that green bridges were significantly preferred by large mammals such as red deer and wild boar but also in the case of roe deer compared to other types of WCSs. This result is supported by other studies that show a preference for wildlife overpasses by large ungulates and large carnivores compared to underpasses (Clevenger and Waltho 2005; Kusak et al. 2009; Simpson et al. 2016; Mysłajek et al. 2020). A rare record of a golden jackal was observed on a grey overpass. Surprisingly, the European badger was recorded only on the overpasses, although it was also found in the surroundings along the ecological corridors. The average daily crossing rate for European badger, red fox, marten and European hare was higher on overpasses compared to underpasses. Mysłajek et al. (2020) showed similar results for European badger and red fox, but the opposite in the case of the European hare and marten, which preferred underpasses.

d) Needs for planning and protection of ecological corridors in the landscape

The identified routes of ecological corridors using the integrated GIS-approach may not coincide with actual wildlife migration routes because model results are affected by the accuracy, updating of the input layers and the assumptions

made on animal behaviour regarding the surface resistance. Furthermore, it depends primarily on the state of the landscape at a certain point in time, which in human-modified landscapes changes considerably over time, as well as on a number of other factors. For example, “least cost path” analyses should not be used for management in landscapes without knowledge of actual migration route data and potential risks of movement across the landscape (Fahrig 2007). Based on the above, frequent updating of input data, like migration routes and species occurrences is recommended for modelling ecological corridors, as well as the precise coordination and targeting of policy, legislative and spatial planning tools to protect ecological corridors.

The need for defragmentation of the European landscapes is currently receiving considerable attention, which has led, i.e. to the development of the European Defragmentation Map (EDM), which provides an overview of the ecological core areas and the connecting ecological corridors within and between member States. So far, this map integrates data for 17 European countries and 2 transnational areas (Böttcher et al. 2022). To reduce barrier effects from the Trans-European Transport Network (TEN-T) the EDM allows to estimate the extent of current and future fragmentation and indicates priority sections for implementing mitigation measures such as the construction of wildlife crossings to restore and reconnect habitats (Reck et al. 2023b). Our results support these efforts by contributing in-situ field data on two important trans-European migration corridors, namely the Bohemian Forest-Northern Alps corridor and the Alpine-Carpathian corridor, to this Europe-wide initiative.

Conclusions

Our study indicates considerable diversity and activity of mammal species as well as aspects of functional connectivity on ecological corridors in two pilot areas in Austria. Applying the ecological stability coefficient (CES), the influence of land use intensity and the related importance of the presence of vegetation cover was shown – the number of species recorded and their average daily activity increased with the CES value. Species richness increases with greater distance from built-up areas or infrastructure. The green bridges (wildlife overpasses) achieve the highest efficiency compared to other WCSs covered, but this difference in efficiency is influenced by the parameters of the individual WCSs. The present study also underlines the strong influence of human activity in the vicinity of WCSs on species richness and mammal activity.

Green bridges have proven to be an effective type of WCS that significantly supports crossing for multiple species. However, in planning and design (not only in the pilot areas in Austria) the long-term provision of comprehensive connectivity to both ecological corridor routes and important landscape features should not be neglected.

The issue of habitat fragmentation and landscape change is currently gaining in importance, due to its relevance for biodiversity loss. Human infrastructure and other associated obstacles pose essential problems and challenges for many animals. The examined ecological corridors in Austria indicate that, in addition to structural connectivity, the quality of functional connectivity is also of crucial importance, especially with regard to sensitive species such as large mammals, as insufficient functional connectivity results in reduced permeabili-

ty. Last but not least, we emphasise that the issue of landscape connectivity is becoming increasingly important and therefore further studies are necessary, taking into account global, regional and local factors.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: CP, MJ. Data curation: MJ. Formal analysis: MJ, RA. Funding acquisition: FD, RG, MJ. Investigation: MJ, CP. Methodology: CP, MJ, RG. Project administration: RG, MJ, CP, FD. Resources: FD, MJ, PČ, RA, CP. Supervision: PČ, CP, RG, TM. Validation: CP, MJ, PČ, FD. Visualization: RA, MJ. Writing - original draft: MJ. Writing - review and editing: FD, CP, RA, PČ, TM, TB.

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Data availability

All of the data that support the findings of this study are available in the main text.

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